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Estimation of social genetic effects on feeding behaviour and production traits in pigs

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ABSTRACT

Pigs are housed in groups during the test period. Social effects between pen mates may affect average daily gain (**ADG**), backfat thickness (**BF**), feed conversion rate (**FCR**), and the feeding behaviour traits of pigs sharing the same pen. The aim of our study was to estimate the genetic parameters of feeding behaviour and production traits with statistical models that include social genetic effects (**SGEs**). The data contained 3075 Finnish Yorkshire, 3351 Finnish Landrace, and 968 F1-crossbred pigs. Feeding behaviour traits were measured as the number of visits per day (NVD), time spent in feeding per day (TPD), daily feed intake (DFI), time spent in feeding per visit (TPV), feed intake per visit (FPV), and feed intake rate (FR). The test period was divided into five periods of 20 days. The number of pigs per pen varied from 8 to 12. Two model approaches were tested, i.e. a fixed group size model and a variable group size model. For the fixed group size model, eight random pigs per pen were included in the analysis, while all pigs in a pen were included for the variable group size model. The linear mixed-effects model included sex, breed, and herd*year*season as fixed effects and group (batch*pen), litter, the animal itself (direct genetic effect (**DGE**)), and pen mates (SGEs) as random effects. For feeding behaviour traits, estimates of the total heritable variation ($T^2 \pm SE$) and classical heritability ($h^2 \pm SE$, values given in brackets) from the variable group size model (e.g. period 1) were 0.34 ± 0.13 (0.30 ± 0.04) for NVD, 0.41 ± 0.10 (0.37 ± 0.04) for TPD, 0.40 ± 0.15 (0.14 ± 0.03) for DFI, 0.53 ± 0.15 (0.28 ± 0.04) for TPV, 0.66 ± 0.17 (0.28 ± 0.04) for FPV, and 0.29 ± 0.13 (0.22 ± 0.03) for FR. The effect of social interaction was minimal for ADG ($T^2 = 0.29 \pm 0.11$ and $h^2 = 0.29 \pm 0.04$), BF ($T^2 = 0.48 \pm 0.12$ and $h^2 = 0.38 \pm 0.07$), and FCR ($T^2 = 0.37 \pm 0.12$ and $h^2 = 0.29 \pm 0.04$) using the variable group size model. In conclusion, the results indicate that social interactions have a considerable indirect genetic effect on the feeding behaviour and FCR of pigs but not on ADG and BF.

Implications

Social interaction between group-housed pigs is a very important component for traits related to feeding behaviour, productivity, and well-being. Genetic variation in traits incorporating social interactions can be estimated using models that include both direct genetic and social genetic effects between pen mates. According to our results, the social genetic effect was important for certain feeding behaviour traits. In particular, the social genetic effect was significant for the feed conversion trait. Thus, accounting for social genetic effect in selection is beneficial for improving the feed conversion rate.

Introduction

Social interactions between animals may affect the health and productivity of livestock housed in groups. For example, cooperation has positive effects on the well-being and productivity of group members, while competition and aggression have adverse effects (Ellen et al., 2014). Aggressive behaviour is usually caused by either ranking disputes in group hierarchy or by competition for limited resources (e.g. feeding). Even though skin injuries and stress are the most notable outcomes of aggression in group-housed pigs, aggressive behaviour also decreases production (Marchant-Forde and Marchant-Forde, 2005; Rydhmer et al., 2013; Camerlink, 2014).

The effects of social interactions may be partly genetic and modelled by a social genetic effect (**SGE**) (also referred to as indirect genetic effects) (Moore et al., 1997) or associate effect (Griffing, 1967). Pigs are a typical example of livestock housed in groups both in commercial settings and at test stations. Several studies have shown that SGE is important in pigs. For example, according to Canario et al. (2010), SGE contributes 44% of the heritable variation in average daily gain (**ADG**) also Nielsen et al. (2018a) found a significant SGE for ADG. In contrast, Bouwman et al. (2010) did not find a find a significant SGE in ADG. Herrera-Cáceres et al. (2019) reported a significant SGE in feed conversion rate (**FCR**), and Bergsma et al. (2008) reported a significant SGE in

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backfat thickness (**BF**) and daily feed intake (DFI). However, little is known of the importance of SGE on feeding behaviour traits. Feeding behaviour traits, such as the number of visits to a feeder per day and feeding speed, are expected to depend on the social behaviour of pen mates. In a recent study, Herrera-Cáceres et al. (2019) found a considerable SGE in the number of visits per day (NVD) and feed intake rate (FR) but not in the time spent in feeding per day (TPD).

Modelling SGE in the context of quantitative genetics has been presented by Griffing (1967), Muir and Schinkel (2002), and Bijma et al. (2007a). In an SGE model, the phenotypic value of an animal depends on its direct breeding value and the sum of the social breeding values of its group mates plus the corresponding non-heritable direct and social effects. Total breeding value of an animal is the sum of its direct breeding value and its own social breeding values towards group mates. The variance of total breeding value depends on the (co)variance components of direct breeding value and social breeding values but also on group size (Bijma et al., 2007a, 2007b). In socially affected traits, the proportion of total breeding value variance over the total phenotypic variance is the measure for inheritable variation preferred over the classical heritability.

Statistical modelling and estimation of variance components in an SGE model are relatively easy with existing variance/covariance estimation programmes when all groups have the same number of animals, i.e. the group size is constant. In practice, group size often varies in commercial settings within and between farms but also at test stations. Even when the aim is to include groups of equal size during the test period, group (batch*pen) size may vary due to several reasons. Variable group sizes pose challenges in estimating variance components for the direct and SGEs using existing variance component estimation programmes. Several solutions have been proposed for coping with variable group sizes (e.g. Arango et al., 2005; Hadfield and Wilson, 2007; Bijma et al., 2007a; Nielsen et al., 2018a).

Given the limited number of publications related to the importance of SGE in feeding behavioural traits in general and in Finnish commercial pig breeds, the objective of our study was to estimate genetic parameters of feeding behaviour and production traits in Finnish pig breeds using a model with an SGE. Estimation and comparison of the magnitude of T^2 and h^2 were our main interests. We also compared the fixed group size SGE model to the more complicated variable group size SGE model.

Material and methods

Data

The data were provided by Figen Oy (Pietarsaari, Finland) and included the feeding and production records of pigs from the central test station from 2011 to 2016. Table 1 shows the ages and weights of the animals during their test periods with the slaughter records.

Pigs arrived at the test station on Tuesday or on Wednesday, and the test started on Saturday. The grouping of pigs to different pens was done according to the arrival weight (same size) and sex (only boars or combination of gilts and castrates) of the pigs. Feeding was *ad libitum* consisting of two commercial feedstuffs. The proportion of the two feedstuffs was based on the growth rate curve of an average pig from the previous test periods. The piggery has automated air conditioning and ventilation based on the age of the pigs and outdoor temperature. Artificial light is on from 7 am to 3 pm. The dimension of the pen is 16.8 m^2 with one-third of concrete slats. The feedings were recorded automatically using the Schauer Spotmix with Schauer MLP electronic feeders and MLP manager data management software (Schauer Agrotronic GmbH).

Table 1
Descriptive statistics of the pigs.

	Mean ± SD
Arrival age at test station	89 ± 10 days
Weight at arrival age	34.4 ± 6.4 kg
Total test time	95 ± 3 days
Slaughter age	186 ± 10 days
Slaughter weight	121.2 ± 12.9 kg

The raw data consisted of 28 964 641 observations made from Finnish Yorkshire, Finnish Landrace, and F1-crossbred pigs and included transponder id, date, time of entering the feeder, time leaving the feeder, and feed intake per visit (FPV). Some visits may be missed due to ear tag-related problems, either the feeding system was not able to record the tag properly or some ear tags might have fallen out from pigs. However, these problems are rare (personal communication with the personnel of the test station). In addition, some pigs were removed from the tests due to sickness (e.g. lameness, loss of appetite, etc.). Otherwise, the thresholds presented in Casey et al. (2005) were applied to remove possible erroneous data. The proportion of outliers was less than 1%. The remaining data contained 28 826 029 observations.

These separate visit observations were used to calculate daily values for the NVD (counts), TPD (min), DFI (g), time spent in feeding per visit (TPV, min), FPV (g), and FR (FR = FPV/TPV, g/min). The final records used in variance component estimation were calculated as averages of the daily records for five test periods of 20 days each: 0–20, 21–40, 41–60, 61–80, and 81–93 days (for more information, see Kavlak and Uimari, 2019). In the following, we use abbreviation where the number indicates the corresponding test period, e.g. NVD1 is NVD from the test period 1, and NVD2 is NVD from the test period 2, etc.

Production traits were ADG (g), FCR (g/g), and BF (mm). For an individual pig, ADG was calculated as the ratio of the difference between last day weight and first day weight within a test period over the duration of the test period in days. Feed conversion rate was measured as feed consumption during the test period measured in feed units divided by the total growth during the test period. Lastly, BF was calculated using the average measurement result of a Hennessy grading probe (type GP4, Auckland, New Zealand), where one sample was taken 8 cm off the midline of the carcass behind the last rib and another 6 cm off the midline between the third and fourth ribs.

Before the statistical analyses, outliers (4 standard deviations of the mean) were removed from the data. The final data included records from 7 394 pigs. The number of animals in pens varied from 8 to 12. Average group size was 9.8. The average additive genetic relationship (r) between the pigs within a group was 0.08, which was estimated using the pedigree data of 11 301 animals with ancestors down to four generations. The average number of offspring with observations per each sire was 16.6.

Statistical analyses

Variance component estimation used a single trait SGEs model. For each trait, two data sets with different requirements from the statistical model were analysed. In the first data, the number of pen mates was restricted to the same fixed number of observations by randomly sampling 8 pen mates with records from each pen. We call this the fixed group size model. In the second data, the number of pen mates was allowed to vary according to the size of the original pen. Only pens where all pen mates had records were included in the analysis. Consequently, numbers of accepted records and pens varied by trait. We call this the variable group size model. Restricted maximum likelihood (**REML**) estimates of variance components were calculated using average information algorithm or AI-REML as implemented in *DMU* software (Madsen and Jensen, 2013). Standard errors to the estimates were taken from the DMU output except for estimates to h^2 and T^2 where Taylor series expansion were used (Dieters et al., 1995).

The social model included sex (5 035 boars, 1 296 gilts, and 1 063 castrates), breed (3075 Yorkshire, 3351 Landrace, and 968 F1 crosses of the two breeds), and herd*year*season (348 classes) as fixed effects, and batch*pen (766 groups), litter (2 862 groups), animal (direct genetic effect (**DGE**) and SGE), and residual as random effects.

$$\mathbf{y} = \mathbf{Xb} + \mathbf{Z}_D\mathbf{a}_D + \mathbf{Z}_S\mathbf{a}_S + \mathbf{Z}_l\mathbf{l} + \mathbf{Z}_g\mathbf{g} + \mathbf{e}$$

where **y** is a vector of observations (feeding behaviour or production), **b** is a vector of fixed effects, **X** is an incidence matrix relating records to fixed effects, $\mathbf{a}_D$ is a vector of random DGE, $\mathbf{a}_S$ is a vector of random SGE, **l** is a vector of random litter effects, **g** is a vector of random group (batch*pen) effects, and **e** is a vector of random residuals; the corresponding incidence matrices are $\mathbf{Z}_D$, $\mathbf{Z}_S$, $\mathbf{Z}_l$, and, $\mathbf{Z}_g$, respectively. The random effects were considered independent except between DGE and SGE:

$$\begin{bmatrix}\mathbf{a}_D\\ \mathbf{a}_S\end{bmatrix} = \mathbf{G}\otimes\mathbf{A}, \quad \text{where } \mathbf{G} = \begin{bmatrix}\sigma^2_{AD} & \sigma_{A_{DS}}\\ \sigma_{A_{DS}} & \sigma^2_{AS}\end{bmatrix}$$

A is the relationship matrix, σ^2_{AD} is the variance of DGE, σ^2_{AS} is the variance of SGE, $\sigma_{A_{DS}}$ is the covariance between DGE and SGE, and ⊗ is the Kronecker product. Litter, batch*pen (group), and residual effects were independently and normally distributed with expected values of **0** and variances of σ^2_l, σ^2_g, and σ^2_e for litter, group, and residual effects, respectively.

The variance of total breeding value (σ^2_{TBV}) (Bijma et al., 2007a, 2007b) is

$$\sigma^2_{TBV} = \sigma^2_{AD} + 2(n-1)\sigma_{A_{DS}} + (n-1)^2\,\sigma^2_{AS}$$

and the total phenotypic variance (σ^2_P) is

$$\sigma^2_P = \sigma^2_{AD} + \sigma^2_g + \sigma^2_l + \sigma^2_e + (n-1)\sigma^2_{AS} + (n-1)r\left[2\sigma_{A_{DS}} + (n-2)\sigma^2_{AS}\right]$$

where n is the average number of pigs in each group and r is the average relatedness within groups ($r = 0.08$). Total heritable variation (T^2) is the ratio $T^2 = \sigma^2_{TBV}/\sigma^2_P$) and classical heritability (h^2) is the ratio $h^2 = \sigma^2_{AD}/\sigma^2_P$.

Results

Phenotypic description

Descriptive statistics of feeding behaviour and production traits are shown in Figs. 1 and 2. In general, the older pigs became, the more frequently they visited the feed station (from NVD1 to NVD5). In contrast, time spent in feeding decreased slightly from 2.9 min (TPV1) to 2.2 min (TPV5). Thus, TPD increased up to 65.2 min/day (TPD2) and then decreased to 54.1 min/day (TPD5). In contrast to NVD and TPD, the rest of the feeding behaviour traits (TPV, DFI, FPV, and FR) increased constantly from period 1 to period 5 (Fig. 1). Mean ADG for the pigs was 946 ± 113 g/d (mean and SD). Corresponding mean values for BF and FCR were 10.7 ± 2.3 mm and 2.5 ± 0.2 g/g, respectively.

Classical heritability

Both estimation models gave the same range of estimates of classical heritability for the feeding behaviour traits: 0.14–0.39 (Tables 2 and 3). For the production traits estimates of classical heritability varied from 0.25 to 0.41 when a fixed group size model was applied and from 0.29 to 0.38 when a variable group size model was applied (Tables 2 and 3). Standard errors of the estimates varied from 0.03 to 0.05. The highest estimates for feeding behaviour traits were obtained for periods 2 and 3.

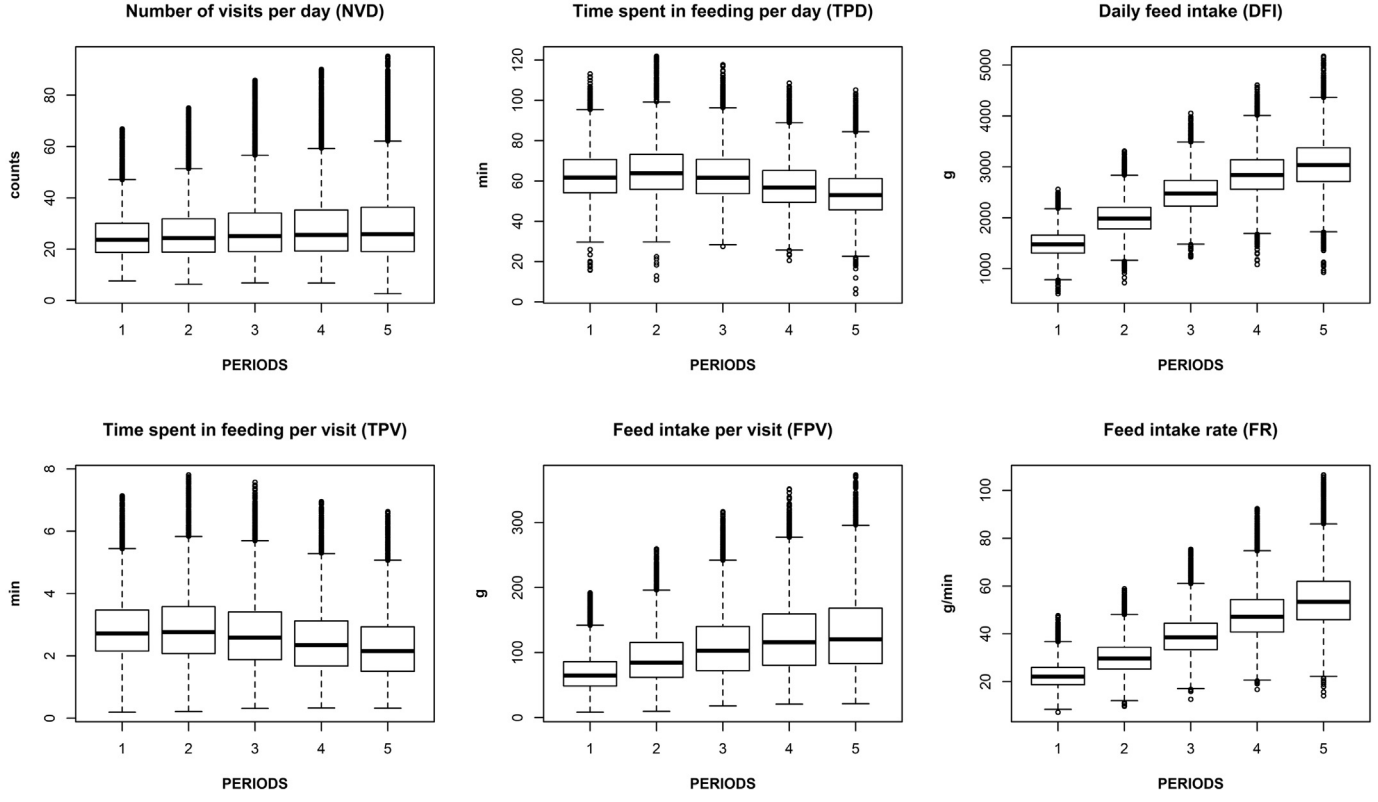

Fig. 1. Box plots of feeding behaviour traits over the five periods in pigs.

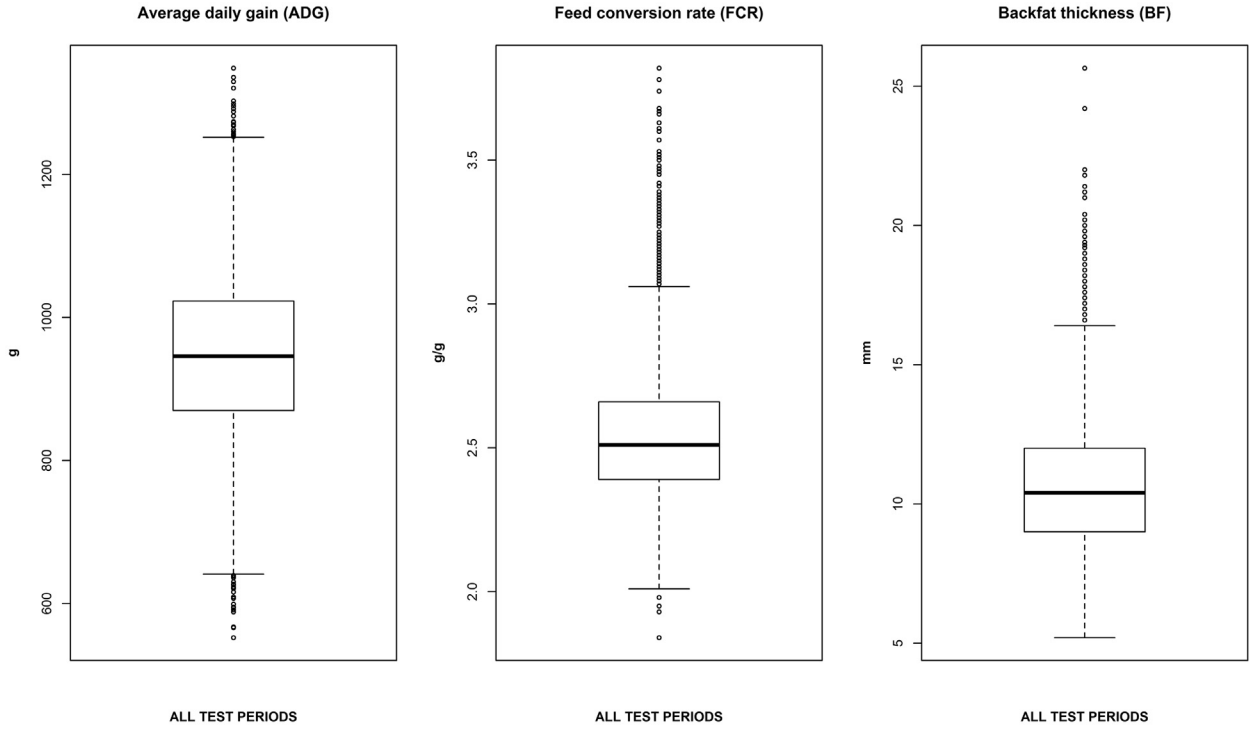

Fig. 2. Box plots of the production traits over the entire test period in pigs.

Variance of social genetic effect and correlation between direct genetic effect and social genetic effect

Variance of SGE (σ^2_{AS}) was generally smaller than the variance of DGE (σ^2_{AD}, Tables 2 and 3). Also, the SEs of the σ^2_{AS} estimates were large. Thus, most of the σ^2_{AS} estimates did not differ from 0 except for TPV and FPV for some traits during certain periods (the significant estimates are bolded in Tables 2 and 3). Most of the significant σ^2_{AS} estimates were obtained in test period 2 (days 21–40 of test). In addition, the SGE variance was small but significant for FCR but not for ADG or BF.

Estimated correlation between DGE and SGE was mostly positive in feeding behaviour traits but not statistically significant (Tables 2 and 3). When a fixed group size model was applied, only TPV1, TPV2, TPV3, TPV4, FPV3, and FPV4 indicated a statistically significant and positive correlation between DGE and SGE. When a variable group size model was applied, the correlation between DGE and SGE was significant only for TPV2 and TPV3. Based on our results, pigs that visit feeders for longer time periods (a genetic potential) also have a positive SGE on the TPV of the pen mates. This relationship was also true for FPV. No statistically significant correlation between DGE and SGE was obtained for the production traits.

Total heritable variation

For feeding behaviour traits, the estimates of T^2 were generally higher than estimates of h^2, ranging from 0.28 ± 0.08 (h^2 = 0.28 ± 0.04) for DFI4 to 0.77 ± 0.13 (h^2 = 0.36 ± 0.04) for TPV3 when a fixed group size model was applied and from 0.17 ± 0.10 (h^2 = 0.27 ± 0.04) for FR3 to 0.85 ± 0.16 (h^2 = 0.34 ± 0.03) for TPV3 when a variable group size model was applied (Tables 2 and 3). For production traits, the estimates of T^2 were similar to the estimates of classical heritability, except for FCR in both the fixed (T^2 = 0.75 ± 0.17 vs. h^2 = 0.25 ± 0.04) and variable (T^2 = 0.37 ± 0.12 vs. h^2 = 0.29 ± 0.04) group size models.

Differences between the models

Estimates and SEs of h^2 were almost identical by the fixed group size and variable group size models (Tables 2 & 3). In addition, estimates of T^2 were similar between the models (the differences between the estimates were within SEs). In production traits, some differences were observed in T^2 between the models, e.g. for FCR the T^2 estimate was 0.75 ± 0.17 using the fixed group size model and 0.37 ± 0.12 using the variable group size model. The difference in estimates of T^2 for FCR is most probably due to different data size; for the variable group size model only pens where all animals had records were included in the analysis (in the fixed group size model all pens with at least eight animals having a record were included in the analysis). In general, a slightly higher correlation between DGE and SGE was obtained from the fixed group size model than from the variable group size model.

Discussion

In this study, we investigated the importance of SGE on feeding behaviour and production traits in Finnish pig breeds. The data were obtained from the test station where animals of two Finnish pig breeds (Finnish Landrace, Finnish Yorkshire) and their F1-crosses were distributed randomly into each pen. Thus, the data did not allow separate analysis of the breeds. This may affect our results if the two breeds differ from each other drastically in terms of the studied traits. However, both are white breeds with similar breeding goals and programmes. Also, based on a previous study of Finnish Yorkshire by Kavlak and Uimari (2019) and Finnish Landraces by Riikimaki (2019), feeding behaviour and estimated heritabilities of feeding behaviour traits were similar between these two breeds. In addition, prior to the SGE model analysis, the same model used in Kavlak and Uimari (2019) was applied for the combined data. The estimated heritabilities were close to those presented in Kavlak and Uimari (2019). Thus, despite the data having two unrelated populations analysed together, we trust that the data provide reasonable and reliable estimates of SGE for feeding

Table 2
Estimates of the genetic parameters from the fixed group size model for feeding behaviour and production traits in pigs.

	N	σ^2_{AD}	σ^2_{AS}	$\sigma_{A_{DS}}$	σ^2_P	$r_{A_{DS}}$	σ^2_{TBV}	h^2	T^2
FBT									
Period 1									
NVD1	7349	22.2 ± 3.1	0.18 ± 0.10	0.32 ± 0.45	74.6	0.16 ± 0.23	35.5	0.30 ± 0.04	0.48 ± 0.12
TPD1	7370	48.7 ± 6.4	0.23 ± 0.14	−0.29 ± 0.72	136.0	−0.08 ± 0.21	55.9	0.36 ± 0.04	0.41 ± 0.09
DFI1	7388	7523 ± 1745	84 ± 83	330 ± 267	53279	0.41 ± 0.35	16259	0.14 ± 0.03	0.31 ± 0.12
TPV1	7372	0.26 ± 0.03	0.002 ± 0.001*	0.01 ± 0.005	0.89	0.57 ± 0.24*	0.49	0.29 ± 0.04	0.55 ± 0.13
FPV1	7390	170.7 ± 25.7	2.2 ± 1.1	4.3 ± 4.0	627.9	0.22 ± 0.20	338.7	0.27 ± 0.04	0.54 ± 0.14
FR1	7378	5.5 ± 0.9	0.08 ± 0.04	−0.12 ± 0.14	25.2	−0.18 ± 0.22	7.7	0.22 ± 0.03	0.31 ± 0.11
Period 2									
NVD2	7352	29.6 ± 3.8	0.15 ± 0.09	0.89 ± 0.55	94.0	0.42 ± 0.25	49.4	0.31 ± 0.04	0.53 ± 0.11
TPD2	7380	65.1 ± 8.2	0.31 ± 0.20	0.73 ± 0.91	166.8	0.16 ± 0.20	90.5	0.39 ± 0.04	0.54 ± 0.11
DFI2	7389	20204 ± 3401	688 ± 208*	781 ± 544	84182	0.21 ± 0.14	64850	0.24 ± 0.04	0.77 ± 0.16
TPV2	7364	0.34 ± 0.04	0.003 ± 0.001*	0.02 ± 0.006*	1.06	0.60 ± 0.20*	0.76	0.32 ± 0.04	0.70 ± 0.13
FPV2	7376	320.1 ± 45.8	4.2 ± 1.9*	10.0 ± 7.0	1121.4	0.27 ± 0.19	665.9	0.29 ± 0.04	0.59 ± 0.13
FR2	7382	10.5 ± 1.6	0.16 ± 0.07*	−0.01 ± 0.25	41.1	−0.01 ± 0.19	18.2	0.25 ± 0.04	0.43 ± 0.13
Period 3									
NVD3	7351	40.4 ± 5.2	0.22 ± 0.13	1.12 ± 0.71	123.4	0.37 ± 0.24	66.9	0.33 ± 0.04	0.54 ± 0.11
TPD3	7380	58.9 ± 7.1	0.26 ± 0.17	0.78 ± 0.81	150.1	0.19 ± 0.20	82.5	0.39 ± 0.04	0.55 ± 0.11
DFI3	7390	34086 ± 5068	375 ± 212	775 ± 698	114742	0.21 ± 0.19	63311	0.30 ± 0.04	0.55 ± 0.14
TPV3	7383	0.37 ± 0.04	0.003 ± 0.001*	0.02 ± 0.006*	1.02	0.56 ± 0.17*	0.79	0.36 ± 0.04	0.77 ± 0.13
FPV3	7386	576.4 ± 76.2	5.7 ± 2.5*	24.0 ± 10.7*	1702.3	0.42 ± 0.19*	1191.7	0.34 ± 0.04	0.70 ± 0.13
FR3	7372	19.1 ± 2.9	0.28 ± 0.15	−0.15 ± 0.43	70.1	−0.06 ± 0.19	30.7	0.27 ± 0.04	0.44 ± 0.14
Period 4									
NVD4	7354	39.3 ± 5.2	0.25 ± 0.16	0.36 ± 0.74	134.4	0.11 ± 0.23	56.6	0.29 ± 0.04	0.42 ± 0.10
TPD4	7377	46.1 ± 5.8	0.42 ± 0.21	0.23 ± 0.75	125.9	0.05 ± 0.17	69.9	0.37 ± 0.04	0.56 ± 0.12
DFI4	7392	42234 ± 6575	90 ± 146	−310 ± 769	152098	−0.16 ± 0.38	42304	0.28 ± 0.04	0.28 ± 0.08
TPV4	7380	0.28 ± 0.03	0.002 ± 0.001*	0.01 ± 0.005*	0.80	0.57 ± 0.18*	0.52	0.35 ± 0.04	0.65 ± 0.13
FPV4	7390	689.3 ± 91.0	6.2 ± 2.8*	27.0 ± 12.3*	2068.9	0.41 ± 0.19*	1371.1	0.33 ± 0.04	0.66 ± 0.12
FR4	7369	29.5 ± 4.4	0.40 ± 0.22	0.25 ± 0.66	106.0	0.07 ± 0.19	52.6	0.28 ± 0.04	0.50 ± 0.15
Period 5									
NVD5	7366	41.2 ± 5.8	0.36 ± 0.21	0.84 ± 0.86	158.6	0.22 ± 0.22	70.6	0.26 ± 0.03	0.44 ± 0.11
TPD5	7376	37.1 ± 5.4	0.17 ± 0.16	0.57 ± 0.70	130.9	0.22 ± 0.26	53.4	0.28 ± 0.04	0.41 ± 0.11
DFI5	7387	55050 ± 8688	1157 ± 515*	1635 ± 1347	226984	0.20 ± 0.17	134633	0.24 ± 0.04	0.59 ± 0.15
TPV5	7382	0.26 ± 0.03	0.001 ± 0.001	0.006 ± 0.004	0.75	0.30 ± 0.22	0.39	0.34 ± 0.04	0.52 ± 0.12
FPV5	7390	802.8 ± 108.6	7.1 ± 3.4*	17.1 ± 14.7	2499.5	0.22 ± 0.19	1390.1	0.32 ± 0.04	0.56 ± 0.12
FR5	7371	39.8 ± 5.9	0.07 ± 0.33	1.1 ± 0.91	143.7	0.22 ± 0.16	58.6	0.28 ± 0.04	0.41 ± 0.16
PT									
ADG	7394	3111.1 ± 492.2	13.5 ± 13.4	−53.0 ± 57.1	10841	−0.25 ± 0.29	3030.6	0.29 ± 0.04	0.28 ± 0.09
BF	6526	1.6 ± 0.22	0.005 ± 0.004	−0.02 ± 0.02	3.9	−0.28 ± 0.17	1.51	0.41 ± 0.05	0.38 ± 0.09
FCR	7340	0.01 ± 0.001	0.0002 ± 0.00009*	0.0004 ± 0.0002*	0.04	0.30 ± 0.17	0.03	0.25 ± 0.04	0.75 ± 0.17

FBT = feeding behaviour traits; PT = production traits; NVD = number of visits per day; TPD = time spent in feeding per day; DFI = daily feed intake; TPV = time spent in feeding per visit; FPV = feed intake per visit; FR = feed intake rate; ADG = average daily gain; BF = backfat thickness; FCR = feed conversion rate; σ^2_{AD} = variance of direct genetic effect; σ^2_{AS} = variance of social genetic effect; $\sigma_{A_{DS}}$ = covariance between direct genetic effect and social genetic effect; σ^2_P = total phenotypic variance; σ^2_{TBV} = variance of total breeding value; $r_{A_{DS}}$ = genetic correlation between direct genetic effect and social genetic effect; h^2 = classical heritability; T^2 = total heritable variation. N = number of observations for each trait. ± indicates the SEs of the estimates. *Statistically significant estimates ($P < 0.05$) of σ^2_{AS}, $\sigma_{A_{DS}}$, and $r_{A_{DS}}$.

behaviour and production traits in these two Finnish pig breeds. However, more precise estimates of SGE variance could have been obtained if the data consisted only one population and the groups were formed with few families per group (Bijma, 2010a; Ødegård and Olesen, 2011).

According to our results, SGE was not statistically significant for most of the feeding behaviour and production traits, except for TPV, FPV, and FCR. The estimates of the total heritable variation for TPV and FPV were generally over 0.5 (±0.17) (depending on the period and method) and 0.4–0.7 (±0.17) for FCR. Using data from a Duroc pig population, Herrera-Cáceres et al. (2019) obtained a significant contribution of SGE for NVD ($T^2 = 0.93 \pm 0.49$ vs. $h^2 = 0.46 \pm 0.09$), DFI ($T^2 = 0.29 \pm 0.29$ vs. $h^2 = 0.25 \pm 0.08$), TPV ($T^2 = 0.67 \pm 0.30$ vs. $h^2 = 0.47 \pm 0.09$), and FR ($T^2 = 0.39 \pm 0.29$ vs. $h^2 = 0.32 \pm 0.08$), while a high negative correlation between DGE and SGE was obtained for TPD (-0.78 ± 0.09), leading to a smaller estimate of T^2 than h^2 ($T^2 = 0.20 \pm 0.19$ vs. $h^2 = 0.27 \pm 0.10$). For the production traits, SGE was less important (for ADG $T^2 = 0.22 \pm 0.18$ vs. $h^2 = 0.22 \pm 0.09$ and for BF $T^2 = 0.51 \pm 0.28$ vs. $h^2 = 0.35 \pm 0.11$) except for FCR ($T^2 = 0.55 \pm 0.43$ vs. $h^2 = 0.24 \pm 0.09$) (Herrera-Cáceres et al., 2019). Based on the data of 14 032 crossbred pigs, Bergsma et al. (2008) obtained a significant contribution of SGE for ADG ($T^2 = 0.71 \pm 0.08$ vs. $h^2 = 0.21 \pm 0.02$), DFI ($T^2 = 0.70 \pm 0.17$ vs. $h^2 = 0.17 \pm 0.03$), and BF ($T^2 = 0.41 \pm 0.04$ vs. $h^2 = 0.35 \pm 0.02$). Nielsen et al. (2018a) estimated SGE of ADG separately for Danish Landrace gilts and boars using a bivariate model and found that the T^2 is stronger between boars (0.32 ± 0.02) than between gilts (0.27 ± 0.01). Thus, our results are in line with other published results and confirm the pattern that SGE is important in feeding behaviour traits (at least in TPV and FPV) and in FCR but less important in BF and ADG.

Although the aim is to have an equal number of pigs in all pens during the test period, the group sizes vary, in our case, mainly because of animals being removed from the test due to health issues (various diseases and leg problems). Also culling of animals from the groups and changing the composition during the test period may cause the variability in SGEs of the animals unless it is taken into account in the model, e.g. by a regression of mean proportion of time spent in a pen or relative space allowance on the studied trait (Ask et al., 2020). However, the effect of including the regression or omitting it did not have a significant effect on estimates of the variance components or h^2 or T^2 (Ask et al., 2020). We did not apply this fine-tuned approach in our analysis. Instead, we first applied a simple model for randomly sampling an equal number of pigs ($n = 8$) from each pen for a fixed group size model and compared these results to those from a variable group size model ($n = 9.8$). The fixed group size model is simpler than the variable

Table 3
Estimates of the genetic parameters from the variable group size model for feeding behaviour and production traits in pigs.

	N	σ^2_{AD}	σ^2_{AS}	$\sigma_{A_{DS}}$	σ^2_P	$r_{A_{DS}}$	σ^2_{TBV}	h^2	T^2
FBT									
Period 1									
NVD1	7091	20.7 ± 2.9	0.15 ± 0.08	−0.50 ± 0.40	69.0	−0.28 ± 0.22	23.7	0.30 ± 0.04	0.34 ± 0.13
TPD1	7208	49.8 ± 6.5	0.18 ± 0.10	−0.46 ± 0.68	134.8	−0.15 ± 0.22	55.8	0.37 ± 0.04	0.41 ± 0.10
DFI1	7335	7660.6 ± 1767.5	93.3 ± 68.2	360.2 ± 261.0	53049	0.43 ± 0.30	21224	0.14 ± 0.03	0.40 ± 0.15
TPV1	7204	0.24 ± 0.03	0.001 ± 0.008	0.007 ± 0.005	0.87	0.43 ± 0.29	0.46	0.28 ± 0.04	0.53 ± 0.15
FPV1	7269	170.4 ± 25.8	2.00 ± 0.88*	4.6 ± 3.8	617.2	0.25 ± 0.20	407.2	0.28 ± 0.04	0.66 ± 0.17
FR1	7350	5.5 ± 0.9	0.06 ± 0.03*	−0.17 ± 0.13	25.0	−0.29 ± 0.24	7.4	0.22 ± 0.03	0.29 ± 0.13
Period 2									
NVD2	7052	28.3 ± 3.8	0.10 ± 0.06	−0.58 ± 0.50	87.5	−0.34 ± 0.30	25.9	0.32 ± 0.04	0.30 ± 0.11
TPD2	7266	63.8 ± 8.2	0.19 ± 0.14	0.11 ± 0.84	164.8	0.03 ± 0.24	80.9	0.39 ± 0.04	0.49 ± 0.12
DFI2	7344	19231 ± 3329	432.3 ± 151.4	392.2 ± 497	83637	0.14 ± 0.17	59616	0.23 ± 0.04	0.71 ± 0.18
TPV2	7136	0.32 ± 0.04	0.002 ± 0.001*	0.02 ± 0.006*	1.05	0.58 ± 0.22*	0.77	0.31 ± 0.04	0.73 ± 0.16
FPV2	7240	315.5 ± 45.7	3.4 ± 1.5*	5.4 ± 6.7	1100.2	0.16 ± 0.20	676.9	0.29 ± 0.04	0.62 ± 0.16
FR2	7334	10.4 ± 1.6	0.13 ± 0.05*	−0.12 ± 0.24	42.2	−0.10 ± 0.21	18.4	0.25 ± 0.04	0.44 ± 0.15
Period 3									
NVD3	7046	39.1 ± 5.2	0.18 ± 0.10	0.17 ± 0.69	118.5	0.06 ± 0.26	55.9	0.33 ± 0.04	0.47 ± 0.13
TPD3	7276	57.6 ± 7.1	0.17 ± 0.12	−0.10 ± 0.73	147.0	−0.03 ± 0.23	68.9	0.39 ± 0.04	0.47 ± 0.11
DFI3	7354	34236 ± 5082	301 ± 167	824 ± 667	115020	0.26 ± 0.21	72060	0.30 ± 0.04	0.63 ± 0.16
TPV3	7292	0.35 ± 0.04	0.003 ± 0.001*	0.02 ± 0.006*	1.02	0.49 ± 0.18*	0.87	0.34 ± 0.04	0.85 ± 0.16
FPV3	7330	558.6 ± 75.2	5.2 ± 2.1*	18.6 ± 10.4	1685.8	0.35 ± 0.19	1292.2	0.33 ± 0.04	0.77 ± 0.16
FR3	7219	18.1 ± 2.8	0.02 ± 0.04	−0.45 ± 0.32	67.9	−0.75 ± 0.93	11.6	0.27 ± 0.04	0.17 ± 0.10
Period 4									
NVD4	7039	34.9 ± 5.0	0.18 ± 0.12	−0.51 ± 0.68	127.9	−0.20± 0.27	40.1	0.27 ± 0.04	0.31 ± 0.11
TPD4	7252	45.1 ± 5.7	0.10 ± 0.09	−0.75 ± 0.59	121.7	−0.35 ± 0.29	39.6	0.37 ± 0.04	0.33 ± 0.10
DFI4	7373	40623 ± 6432	48 ± 104	342 ± 688	152074	0.24 ± 0.61	50399	0.27 ± 0.04	0.33 ± 0.09
TPV4	7275	0.26 ± 0.03	0.002 ± 0.001*	0.01 ± 0.005	0.81	0.51 ± 0.21*	0.59	0.32 ± 0.04	0.73 ± 0.15
FPV4	7353	674.1 ± 90.5	5.4 ± 2.3*	14.3 ± 11.9	2052.4	0.24 ± 0.20	1342.2	0.33 ± 0.04	0.65 ± 0.14
FR4	7204	28.7 ± 4.3	0.04 ± 0.06	−0.23 ± 0.52	102.7	−0.20 ± 0.46	28.2	0.28 ± 0.04	0.28 ± 0.11
Period 5									
NVD5	7146	40.4 ± 5.8	0.29 ± 0.16	0.73 ± 0.82	153.7	0.21 ± 0.24	76.3	0.26 ± 0.04	0.50 ± 0.14
TPD5	7265	35.5 ± 5.2	0.07 ± 0.09	−0.42 ± 0.59	125.6	−0.27 ± 0.40	33.4	0.28 ± 0.04	0.27 ± 0.10
DFI5	7321	59630 ± 9162	24 ± 156	1212 ± 944	222910	1.00 ± 2.95	82895	0.27 ± 0.04	0.37 ± 0.11
TPV5	7296	0.24 ± 0.03	0.001 ± 0.0008	0.004 ± 0.004	0.76	0.22 ± 0.24	0.42	0.32 ± 0.04	0.55 ± 0.13
FPV5	7352	788.1 ± 108.1	6.0 ± 2.6*	4.5 ± 14.3	2471.0	0.07 ± 0.21	1329.1	0.32 ± 0.04	0.54 ± 0.13
FR5	7193	38.1 ± 5.8	0.17 ± 0.12	0.31 ± 0.73	144.7	0.12 ± 0.29	57.1	0.26 ± 0.04	0.39 ± 0.12
PT									
ADG	7394	3118.2 ± 492.4	17.9 ± 11.1	−76.5 ± 57.3	10833.1	−0.32 ± 0.23	3162.1	0.29 ± 0.04	0.29 ± 0.11
BF	3542	1.6 ± 0.32	0.01 ± 0.008	−0.03 ± 0.04	4.2	−0.22 ± 0.26	2.03	0.38 ± 0.07	0.48 ± 0.12
FCR	6901	0.01 ± 0.001	$0.20\times10^{-5} \pm 3.5\times10^{-5}$*	0.0001 ± 0.0002	0.04	1.00 ± 8.95	0.01	0.29 ± 0.04	0.37 ± 0.12

FBT = feeding behaviour traits; PT = production traits; NVD = number of visits per day; TPD = time spent in feeding per day; DFI = daily feed intake; TPV = time spent in feeding per visit; FPV = feed intake per visit; FR = feed intake rate; ADG = average daily gain; BF = backfat thickness; FCR = feed conversion rate; σ^2_{AD} = variance of direct genetic effect; σ^2_{AS} = variance of social genetic effect; $\sigma_{A_{DS}}$ = covariance between direct genetic effect and social genetic effect; σ^2_P = total phenotypic variance; σ^2_{TBV} = variance of total breeding value; $r_{A_{DS}}$ = genetic correlation between direct genetic effect and social genetic effect; h^2 = classical heritability; T^2 = total heritable variation. N = number of observations for each trait. ± indicates the SEs of the estimates. *Statistically significant estimates ($P < 0.05$) of σ^2_{AS}, $\sigma_{A_{DS}}$, and $r_{A_{DS}}$.

group size model. In theory, random sampling of pen mates from the complete data for the fixed group size model can be expected to decrease the amount of information for the data analysis. However, simpler models tend to behave better numerically and allow the use of a wider range of software. When the variable group size model was used to analyse the full data, we observed that traits DFI5, TPD4, and FCR showed no convergence using AI-REML, nor using EM-REML, in sufficient time after several restarts using either already reached or different starting values. In these traits, the correlation between direct and SGEs was estimated to be one or almost one. No such convergence problems were observed using the fixed group size model. Overall, both models gave similar estimates and SEs of the variance components; the small differences between estimates were within the SEs. As a tendency, the fixed group size model gave higher estimates of the correlation between DGE and SGE than the variable group size model. Again, the differences in estimates between the two models were within the SE. Based on our results, a simple fixed group size model with a random selection of pen mates is useable for estimation of variance components even when the actual group size varies.

Social genetic effects among group mates may depend on group size: social interaction between animal pairs are weaker in a large group than in a small group (Arango et al., 2005). The dependency between group sizes and variances has been discussed in Bijma (2010b), where he also proposed a method to account for this dependence with a dilution parameter (d) that is trait dependent and has a value of 0 if SGE does not depend on group size and a value of 1 if SGEs are inversely proportional to group size, i.e. group member influences are diluted in large groups. Because the minimum group size in our data was 8 and the maximum was 12, our model may benefit from a dilution parameter. Therefore, we tested two dilution parameters: d = 0.5 and d = 1 (results not shown). In general, the estimated heritability stayed about the same. However, small differences (within SEs) appeared in the covariance between DGEs and SGEs leading to changes in T^2. Moreover, correlations between the diluted and nondiluted heritability and total heritable variation estimates were both over 90%. Certain field data analyses with the dilution parameter have been published (Canario et al., 2010; Nielsen et al., 2018b), but Duijvesteijn et al. (2012) did not find a dependency between the magnitude of SGE and the group size. Also, precision of the estimates of the dilution parameter may be low if the coefficient of variation in the group size is low (Heidaritabar et al., 2019).

When SGE has a significant contribution to the total heritable variance (T^2), it is important to consider social interactions between animals in a selection programme. Selection methods that ignore SGE may lead to unexpected response to selection, especially if DGE and SGE are negatively correlated (Bijma et al., 2007a). As an example of a

benefit of including SGE in a breeding programme, Bijma et al. (2007b) estimated that when properly accounting for social interactions, a three-fold higher total heritable variation and potential response to selection may be obtained in a layer chicken population in terms of mortality caused by pecking behaviour than with a breeding programme that ignores SGE. Also, Ellen et al. (2014) demonstrated that selection for SGE is promising in many species, e.g. cattle, cod, deer, mice, mink, and pigs. To optimize SGE estimation, the number of groups should be reasonably large (Bijma, 2010a). Thus, SGE estimation is difficult in breeding programmes where data are collected from farms with a single group such as cattle (Ellen et al., 2014). Based on our results, including SGE in the estimation model for FCR, a higher response to selection may be obtained compared to the currently applied selection based purely on DGE.

Conclusion

In this study, we investigated the importance of accounting for SGE using two statistical models (fixed or variable group size) for feeding behaviour and production traits in Finnish pig breeds. The two models gave similar estimates of the variance components. Among the studied feeding behaviour traits, SGE was significant only for TPV and FPV. For these traits, the difference between T^2 (around 0.7) and h^2 (around 0.3) was large. However, these traits are generally not important in breeding programmes. The opposite is true for FCR, which is very important in most pig breeding programmes. Based on our and other published results, SGE should be accounted for in breeding value estimation of FCR and exploited in selection. Fortunately, there is no evidence of negative correlation between DGE and SGE for FCR. Thus, ignoring SGE in breeding programmes and selecting purely on DGE does not cause negative effects on social interactions that may affect FCR in the long run.

Ethics approval

The data were received from the test station. No animal experiment was needed in this project, so no ethical approval is required. The project follows the University of Helsinki research ethical guidelines, good scientific practice, and all applicable laws and regulations.

Data and model availability statement

The data set and software used in this study are not publicly available but may be available from the owner of the data (Figen Oy, Finland) and from the owner of the software (Natural Resources institute Finland, LUKE) on reasonable request.

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Declaration of interest

The authors declare no conflict of interest.

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